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Postglacial spatiotemporal peatland initiation and lateral expansion dynamics in North America and northern Europe

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Abstract

Peatlands are major ecosystems of the northern hemisphere and have a significant role in global biogeochemical processes. Consequently, there is growing interest in understanding past, present and future peatland dynamics. However, chronological and geographical data on peatland initiation are scattered, impeding the reliable establishment of postglacial spatiotemporal peatland formation patterns and their possible connection to climate. In order to present a comprehensive account of postglacial peatland formation histories in North America and northern Europe, we collected a data-set of 1400 basal peat ages accompanied by below-peat sediment type interpretations from literature. Our data indicates that all peatland initiation processes (i.e. primary mire formation, terrestrialization and paludification) co-occurred throughout North America and northern Europe during the Holocene, and almost equal amounts of peatlands formed via these three processes. Furthermore, the data suggests that the processes exhibited some spatiotemporal patterns. On both continents primary mire formation seems to occur first, soon followed by terrestrialization and later paludification. Primary mire formation appears mostly restricted to coastal areas whereas terrestrialization and paludification were more evenly distributed across the continents. Primary mire formation seems mainly connected with physical processes, such as ice sheet retreat. Terrestrialization probably reflected progressive infilling of water bodies on longer timescales but was presumably drought-driven on shorter timescales. Paludification seems affected by climate as it slowed down in Europe during the driest phase of the Holocene between 6 and 5 ka. Lateral expansion of existing peatlands accelerated ca. 5000 years ago on both continents, which was likely connected to an increase in relative moisture.

Key words: northern peatlands, primary mire formation, terrestrialization, paludification, lateral expansion, climate–peatland interactions

Introduction

Peatlands are common ecosystems in the cool and humid climates of the northern hemisphere. High-latitude peatlands can be found in areas where the mean annual precipitation is greater than 500 mm, where the potential evapotranspiration ratio is less than 1 and where mean annual temperatures are between 1.5 and 6 °C (Gignac and Vitt, 1994). The resulting positive effective moisture balance prevents complete decomposition of plant material and causes peat to accumulate (e.g. Charman, 2002 and references therein).

Globally, peatlands cover ca. 3% of the terrestrial land area (e.g. Rydin and Jeglum, 2006). The northern peatland area is estimated to be 4 x 10^6 km^2, which comprises about 90% of the global peatland area (Yu et al., 2010). Despite their relatively low global coverage, peatlands store ca. 30% of global terrestrial carbon (Gorham, 1991) and northern peatlands hold ca. 90% of the total global peatland carbon pool (Yu, 2011). Wetlands are the strongest natural methane (CH_4) source and contribute 75% to the atmospheric concentration from natural sources (e.g. Ehhalt et al., 2001). High-latitude peatlands are estimated to account for 34–60% of global wetland CH_4 emissions (Bartlett and Harris, 1993; Matthews and Fung, 1987). Thereby, northern peatlands play an indisputable and significant role in Earth’s carbon cycle and in other biogeochemical processes.

Due to the importance of peatlands in the global carbon budget, there is growing interest in the reconstruction of the Holocene peatland extent, the associated carbon accumulation and the influence of these on the global carbon cycle (e.g. Kleinen et al., 2012). Large data-sets of peat initiation dates alone have been compiled by e.g. Gorham et al. (2007), Korhola et al. (2010), MacDonald et al. (2006), and Smith et al. (2004). Yet these hemispheric studies do not portray the peatland formation pathways and their subsequent development. A few regional-scale estimations (e.g. Huikari, 1956; Korhola and Tolonen, 1996) and studies (Kuhry and Turunen, 2006) have been presented on the origin and development of peatlands in northern Europe and North America during the Holocene, but comprehensive large-scale data compilations that disentangle the peatland initiation processes are not available.

Peatland formation can initiate via three processes: primary mire formation, terrestrialization or paludification. In primary mire formation peat is formed directly on wet mineral soil when the land is *newly exposed* due to crustal uplift or deglaciation (e.g. Rydin and Jeglum, 2006; Tuittila et al., 2013). Regionally, primary mire formation has been, and still is, a very common peatland initiation process, for example on isostatically uplifting sea shores (Sjörs, 1983).

In terrestrialization and paludification, on the other hand, the area colonized by peatland vegetation has experienced previous sediment deposition or soil development. In the classic autogenic model, terrestrialization proceeds through infilling of a water body with organic and inorganic material over centuries and millennia and peatland vegetation colonize the water body, e.g., from its edges as floating peat mats (Charman, 2002; Rydin and Jeglum, 2006 and references therein). Eventually, any water-collecting basin may become infilled and terrestrialized (Charman, 2002). A new conceptual model of episodic, drought-triggered terrestrialization presents the infilling as an allogenic process driven by decadal-to-multi-decadal hydroclimatic variability (Ireland et al., 2012). This model is well supported by numerous case studies (see Ireland et al., 2012). In both terrestrialization models, the trophic status of the water body and the catchment, the bathymetry, and the catchment topography also have a strong influence on terrestrialization (Frenzel, 1983).

In contrast to primary mire formation, in paludification, peatland vegetation colonizes dry mineral soil that is occupied by terrestrial vegetation or *long-exposed* bare land (Kuhry and Turunen, 2006) and peat starts to form without a transitional aquatic phase. The prerequisite is that the local hydrological conditions become wetter, induced for instance by climatic change, fire, or beaver damming, resulting in waterlogged soil conditions that promote peat accumulation (Charman, 2002 and references therein; Gorham et al., 2007; Härkönen, 1999; Rydin and Jeglum, 2006 and references therein; Tuittila et al., 2007).

Independent of the peatland initiation processes, all peatlands may subsequently grow horizontally onto the surrounding land by lateral expansion. Lateral expansion occurs when marginal areas of peatlands become waterlogged due to excess water running off from the peatland surface or from the surrounding area (Charman, 2002 and references therein). This process can be exclusively driven by the autogenic succession of the peatland but favourable climate and topographical conditions can hasten it significantly (e.g. Korhola, 1996). Because of its partly autogenic character, lateral expansion may proceed continually unless it encounters topographical or climatic barriers and thereby slows down or stops. Under favourable conditions it may proceed by several meters per year (Korhola, 1994) or even upslope (Korhola, 1996).

By synthesizing available information from literature we have composed an up-to-date survey of postglacial peatland initiation processes and lateral expansion dynamics, as well as their spatiotemporal patterns in North America and northern Europe. Previously, this information has mostly relied on sophisticated estimations (cf. Sjörs, 1983). Hence, also syntheses of the climate feedbacks of peatland ecosystem development have remained tentative. Data-based information on past peatland formation dynamics could significantly improve our understanding of the sensitivity of peatland ecosystems to climate forcing.

Material and methods

The initiation process or timing cannot be inferred from the present state of a peatland. The initiation processes have to be defined by careful examination of the contact zone between the basal peat and the underlying sediment, and by dating the basal peat. In existing literature, over 3000 basal peat dates are available from more than 2000 high-latitude peatland sites (e.g. Gorham et al., 2007; Korhola et al., 2010; MacDonald et al., 2006; Smith et al., 2004). From these we compiled a new data-set of basal peat radiocarbon ages for North America (henceforth, NA) and northern Europe (NE), with associated sediment type analysis and/or interpretation on the peatland initiation process and lateral expansion. Due to limited accessibility and language barriers most of the Russian data were excluded and only some data from European Russia (west of the Urals) were included.

In our literature based approach we did not carry out any sediment type interpretations but relied on the original publications for their interpretation of the sediment type and the peatland initiation process. In the original studies the type of sediment at the contact zone with the basal peat was determined by stratigraphic analysis, plant macrofossil analysis and/or by measuring the organic matter content (i.e. loss on ignition) of the basal sediments or, in a small number of cases, by visual assessment. We grouped our data into peatlands that initiated through primary mire formation, terrestrialization and paludification according to the following division of the below-peat sediment types. Peat formed through primary mire formation is typically underlain by gravel, sand or clay (i.e. inorganic sediments). Peat formed via terrestrialization is underlain by highly organic limnogenic sediments (e.g. gyttja, sappropel, detritus mud). Peat formed through paludification is underlain by organic material originating from the preceding vegetation communities, such as forest or heath; often macroscopic charcoal particles are present and indicate peat formation after a local fire (Tuittila et al., 2007). On rare occasions paludification has occurred on bare ground, e.g. on moraines that have been exposed for centuries or millennia, and cannot, therefore, be classified as primary mire formation. In cases where the peatland initiation process could not be determined according to the above criteria, e.g. because the stratigraphic description was insufficient, the basal peat ages were not included in our data-set. .

In addition to the peatland initiation processes, we were able to identify lateral expansion of peatlands in our data. In our view it is reasonable to study lateral expansion separately from the initiation processes since it is the ecosystem process by which all existing peatlands may spread and there may be other allogenic forcing factors behind it than in peatland initiation. The identification of lateral expansion is, however, not as straight-forward as with the peatland initiation processes. This is because the underlying sediment of peatlands that have initiated through paludification and those peatland areas formed through lateral expansion are essentially identical. Lateral expansion can be separated from paludification by the examination of the basal peat age distribution pattern in the peatlands. This requires a series of basal peat ages that spatially encompass different parts of the peatland under study. If the basal peat ages become gradually younger from an older, initiation point towards the edges of the peatland, they represent peat formed through lateral expansion (Anderson et al., 2003; Korhola, 1996) (see also Fig. 1). The basal peat ages in our data-set originate from peatlands with both single and multiple dated basal peat cores. Peatlands with only one (or two) basal dates were separated from peatlands with three or more basal peat dates. The latter formed the group of multiple dated peatlands (see Supplementary Table 1, S1). Lateral expansion dynamics can only be identified for peatlands with multiple dated basal peats.

The attempt to create a historical spatiotemporal picture of peatland initiations is complicated by the fact that in some cases now-extant peatlands started to form simultaneously from several separate loci that over time fused together by lateral expansion. This development pattern has been previously discussed by Foster and Wright (1990) where different conceptual bog development models are presented (see Fig. 1b). The initiation process of individual loci is not necessarily the same, as can also be seen in our data (see S1, e.g. Luovuoma peatland in NE by Mäkilä and Moisanen, 2007; Juutinen et al., 2013). Our data also includes examples of the other development models shown in Fig. 1 (see in S1 e.g. Limbergsmossen in Almquist-Jacobsen and Foster, 1995, for Fig. 1a; and Hammarmossen in Foster et al., 1988, for Fig. 1c). In order to keep the peatland initiation data analysis as explicit, simple and intercomparable as possible in this study, we only included the oldest basal peat date and the associated initiation process per peatland, regardless of the number of initiation loci, for the peatland in question. This ensures that single- and multiple-dated peatlands, and the factors controlling their initiation, are treated equally in the data. If peatland patches form in very close proximity to each other it might be impossible with this kind of data to assess whether the driving factors behind the initiation of a peatland patch are allogenic or a result of the changed moisture conditions brought about by another peatland growing in close proximity. All data, including the excluded initiation data, are, however, shown in the supplementary data (S1, dates included in initiation analysis are marked with an asterisk).

The initial radiocarbon ages were calibrated to calendar years using IntCal09 (Reimer et al., 2009) in OxCal 4.1. (Bronk Ramsey, 1995, 2009) and rounded to the nearest decade. The results are presented in S1. We analysed the compiled data-set by the raw number of initiation dates and peatland formation processes. Based on the basal peat dates, their position in the peatland, and sediment type interpretation a value of peatland initiation process and lateral expansion was then assigned. To illustrate regional differences in peatland dynamics we produced spatial representations of the data-set in ArcGIS (Figs 4, 5 and 7). In addition, we calculated probability density functions (PDFs) for each calibrated age in our data-set in OxCal 4.1. We generated in OxCal 4.1 summed probability curves for various subsets (e.g. radiocarbon ages representing a specific peatland formation process) by summing the relevant age-specific PDFs to illustrate the temporal trends and frequencies of peatland formation dynamics.

We acknowledge that there are numerous complications related to our literature-based approach on peatland initiation. For example, we cannot assess whether the published basal peat ages truly represent the contact zone of the peat to the underlying sediment, or even if the dated basal peats have been collected from the oldest parts of the peatlands and thereby really represent the first initiation of the peatlands. There are also possible errors related to the radiocarbon dating of the basal peat samples but this is taken into consideration when presenting the temporal trends as summed probability curves in Figures 2 and 6. In a very few cases (less than 10 in the whole data-set), the publications did not provide original lithological information. In these cases we used the initiation process reported in the study. Another evident limitation of the data-set originates from the selection of study sites in the original studies, which probably results in biased representativeness of available data. For example, young peatlands or peatlands in terrain that is difficult to access are most likely under-represented.

In order to further assess the significance of these possible error sources listed above we carried out sensitivity analysis to our data. The temporal trends in the present data with below-peat sediment type interpretation were compared to trends in all available basal peat data (Korhola et al., 2010) to see how well our data-set represents all available data. In addition, high quality subsets (marked with an “S” in S1) composed of basal peat dates with the most reliable information on the initiation process (determined by stratigraphic analysis and/or plant macrofossil analysis of the below-peat sediment type) were compiled and compared with the whole data on each initiation process. The robustness of the lateral expansion trends was assessed by comparing the data to a subset of peatlands with ≥ 7 lateral expansion dates per peatland.

We are confident that even with some data-point-specific uncertainties, the whole assembled data-set can capture salient Holocene-scale spatial and temporal trends in peatland formation dynamics and can thus provide important new information. Our results may function as a basis for further assessments and meta-analyses of the initiation and development history of northern peatlands.

Results and discussion

Our data compilation yielded a total of 1450 basal peat ages with sediment type interpretations from 694 peatlands (see S1) in boreal, subarctic and arctic Europe and North America. Figures 2a and b show that the present data-set is highly representative of all available basal peat ages presented in Korhola et al. (2010) in NA and NE. In addition, we have included some new data from NE that was not present in Korhola's et al. (2010) data-set. The current data-set enables us to present results on the proportion of peatland initiation processes, their spatial and temporal distribution, and lateral expansion dynamics during the Holocene. Figures 2c and d underline the need to discuss peatland initiation processes and lateral expansion dynamics separately, since these have obvious differences in their temporal patterns with peatland initiation being more pronounced during the early Holocene and lateral expansion more prominent in the late Holocene. In addition, we explore the sensitivity of peatland ecosystems to climate forcing on broad temporal and spatial scales, only enabled by such continental-scale data-sets.

Proportion and spatial distribution of peatland initiation processes

According to our results, the proportion of the three peatland initiation processes do not vary significantly on a broad scale, but their occurrence exhibits spatial patterns. In NA, all peatland initiation processes seem to have occurred to a similar extent during the Holocene; with terrestrialization (38%) and primary mire formation (36%) as the leading processes (Fig. 3a). The initiation processes exhibit spatial patterns so that primary mire formation is largely restricted to coastal areas, whereas terrestrialization and paludification are more evenly distributed across the continent (Fig. 4a). On a regional scale our data is in agreement with previous estimations from west-central Canada where paludification was reported to be the prevalent peatland initiation type (71%) and terrestrialization represented the remainder (28%) (Kuhry and Turunen, 2006) (Fig. 4a). However, our continental-scale survey shows that the estimations by Kuhry and Turunen (2006) cannot be widely extrapolated since on a continental scale for example paludification accounts for only 26% of NA peatland initiation. Furthermore, the data suggest that terrestrialization has also occurred widely in Arctic areas (Fig. 4), which differs from some previous studies which have suggested that terrestrialization is uncommon in those areas (Tarnocai and Zoltai, 1988).

Also in NE the initiation processes seem to have been almost equally common (Fig. 3b). The data suggest that paludification was the most common peatland initiation type (ca. 40%) (Fig. 3b), and it occurred uniformly around the continent (Fig. 4b). Primary mire formation (31%) seems to have been mainly restricted to coastal and mountainous areas (Fig. 4b). Earlier estimations for instance for Finland have proposed slightly higher proportions for primary mire formation, i.e. 35–50% (Huikari, 1956) and 40–60% (Korhola and Tolonen, 1996). The current data show that in NE, terrestrialization has been a distinctly more common peatland initiation process than postulated before. For example, previous estimations for terrestrialization in Finland have ranged from 5–15% (Lappalainen and Toivonen, 1985). According to our data terrestrialization (29%) occurred throughout the continent but was especially prominent on the shores of the Gulf of Finland (Fig. 4b).

Paludification has been considered responsible for producing vast areas of peatlands and therefore it has been proposed as the most important peatland forming process in the northern hemisphere (e.g. Sjörs, 1983). This is true, especially if lateral expansion is included in paludification. In our approach where paludification (initiation process) is separated from lateral expansion, the latter emerges as the most important process forming new peatland *areas*. It is beyond the scope of this article to accurately determine the areal extent of peatlands initiated through each initiation process. Although in general, peatlands initiated through terrestrialization often occupy relatively small, geographically isolated patches whereas peatlands initiated through paludification on flat terrain may form vast interconnected peatland complexes (e.g. Charman, 2002; Sjörs, 1983; Tiner, 2003).

Spatiotemporal patterns of peatland initiation and lateral expansion in NA and NE

Our data-set suggests that all peatland initiation processes have co-occurred on both continents throughout the Holocene. The spatiotemporal pattern of peatland initiation in NA and NE is shown in Figures 5a and b, respectively, whereas the temporal trend of the initiation frequencies is shown in Figure 6. The first signs of peatland formation on the ice-free areas of NA have been reported at almost 20 ka (Gorham et al., 2007). In our data the oldest dates are ca. 13 ka and depict primary mire formation and terrestrialization (Figs 5a and 6a). At first, peatland initiation was mostly confined to coastal and mountainous areas (Fig. 5a) as has also been suggested by Gorham et al. (2007). According to our data, peatlands started to form more commonly through terrestrialization and paludification in the interior parts of the continent with a time-lag of a few thousand years, i.e. 11–9 ka, (Fig. 5a). This has also been previously observed by Gorham et al. (2007) and Halsey et al. (1998). Primary mire formation seemed to decrease in NA from its initial early Holocene high values but increased again 8–5.5 ka especially around the Hudson Bay area (Figs 5a and 6a). At 5–4 ka terrestrialization seemed to be the most important peatland initiation process in the central parts of the continent, concentrating around the Great Lakes, Lake Winnipeg and the watershed of Saskatchewan River (Fig. 5a). The data suggest that during the last 4 ka, low-intensity peatland initiation has continued via all processes throughout the continent (Figs 5a and 6a) with similar spatial distribution patterns as in the earlier Holocene. However, in the most recent millennia peatland initiation may have concentrated on the eastern half of the continent (Fig. 5a).

The NE peatland initiation pattern seems to concur in part with the NA pattern: primary mire formation was the first Holocene peatland initiation process (Fig. 6b) and it was mostly restricted to coastal areas (Fig. 5b). However, in contrast to peatland initiation in NA initiation in NE, regardless of the pathway, apparently started directly over wide areas after the retreat of the Scandinavian ice-sheet 11–9 ka (Figs 5b and 6b) without an extended time-lag as seen in central NA (Fig. 5 and Halsey et al., 1998). The 10–8 ka time window seems the most intensive phase of new peatland initiation throughout the continent (Fig. 5b) after which primary mire formation and terrestrialization in particular slowed down (Fig. 6b). After 5 ka, and specifically 4–3 ka, peatland initiation accelerated again through paludification (Fig. 6b). Over the last 4 ka, paludification appears as the most important peatland initiation process in Europe and has occurred widely in the northern regions of the continent (Fig. 5b).

The continuous peatland initiation during the late Holocene (Figs 5 and 6) suggests that the straight-forward decline in peatland initiation rates following the early Holocene as proposed, for example by Gorham et al. (2007), MacDonald et al. (2006) and Smith et al. (2004), does not occur. Furthermore, when our lateral expansion data is included in the peatland initiation rates, it seems that the formation rate of new peatland *area* was still high 5–1 ka, especially in NA (Fig. 6), and not significantly lower than in the early Holocene. Moreover, the widespread occurrence of paludification in recent times does not support the claim that at present and during the recent past the formation of new peatlands occurred mainly via terrestrialization, or was restricted to areas facilitating primary mire formation, such as coastal areas (cf. Franzén, 1994). As the subset of high quality peatland initiation dates and the subset of lateral expansion with ≥ 7 lateral expansion dates/peatland (blue curves in Fig. 6) exhibits quite the same temporal trends as our whole data (red curves in Fig. 6), we consider our data-set to be reliable and representative of peatland initiation and lateral expansion on the continents.

Figure 7 shows the spatiotemporal lateral expansion of existing peatlands. The data suggest that in the early Holocene, lateral expansion was restricted to the western and eastern shores of NA and to southern Finland in NE. Lateral expansion seems quite intense and widespread in NE for the first part of the Holocene (Figs 6b and 7), while in NA lateral expansion was apparently restricted to the more coastal areas until ca. 7 ka (Fig. 7). After this, peatlands spread intensively also in the central parts of NA, especially from around 5.5 ka until the last millennium. The most intense and widespread phase of lateral expansion in NE apparently occurred around 5–3 ka, but in some areas it has also continued strongly through the last millennia (Figs 6 and 7).

Noteworthy, all peatland formation frequencies on both continents seem to decrease towards the present, being especially slow during the last 2 ka, with the exception of paludification and primary mire formation in NA (Fig. 6). This most likely mainly reflects the under-representation of young peatlands in the data because research traditions favour older peatlands and avoid young marginal areas (Korhola et al., 2010; Kuhry and Turunen, 2006). Also, some areas covered by vast peatlands, such as the Hudson Bay Lowland, remain clearly under-represented due to scarcity of data. These factors may bias our results.

Exploring the linkage of climate and physical processes to peatland initiation processes and lateral expansion

Peatlands are complex ecosystems and their development is controlled by varying external (allogenic) forcing factors (e.g. climate and fire) and internal (autogenic) processes (e.g. hydrology and peat thickening through autogenic succession) on local to continental spatial scales. These processes operate simultaneously and it is challenging to differentiate their contributions to peatland development (Tuittila et al., 2007). However, if peatlands of different size, age and maturity stage show a similar response, e.g. increased rates of lateral expansion, at a regional or wider scale, this can be interpreted as a response to a strong change in external forcing factors, such as climate (e.g. Charman et al. 2013; Korhola, 1996). Peatlands react to climate variability on millennial, centennial and decadal scales (e.g. Bridgham et al., 2008; Chapin et al., 2000; Ireland et al. 2012; Korhola et al., 1996; Roulet et al., 2007). Here we will discuss millennial-scale continental changes.

Primary mire formation

Our data indicate that primary mire formation was not directly linked to millennial-scale Holocene climate variations, although positive effective moisture conditions had to prevail for it to start. The spatiotemporal pattern of primary mire formation in our data suggest that physical processes related to ice sheet retreat and the following isostatic uplift enabled primary mire formation to take place on exposed water logged land on alluvial ground. In NE the Scandinavian ice sheet disappeared ca. 10 ka from the Bay of Bothnia on the Baltic Sea and surrounding land areas (Eronen et al., 2001), which is seen as an intensification of primary mire formation in the area (Figs 5b and 6b). Afterwards the process was restricted to mountainous areas and isostatically uplifting sea shores (Fig. 5b) and gradually slowed down (Fig. 6b).

In NA, however, the disappearance of the Laurentide Ice Sheet (LIS) and the subsequent primary mire formation seems to have been more complex. In the beginning of the Holocene primary mire formation was concentrated on the sea shores that had just been exposed by the retreating ice sheet or by isostatic uplift (Fig. 5a). The frequency of primary mire formation in the time window of 11-8 ka was quite moderate (Fig. 6a) possibly because vast areas were inundated by glacial lakes (Dyke et al., 2003; Gorham et al., 2007). It also seems that the climate became too dry for peatland formation in central NA immediately after the ice sheet retreated (Halsey et al., 1998; Williams et al., 2010), which highlights that primary mire formation is not driven by physical processes alone. The LIS disappeared from North Labrador and the Ungava Peninsula only ca. 7 ka ago (Dyke et al., 2003) after which rates of primary mire formation increased (Fig. 6a) especially on the Ungava Peninsula and the eastern side of Hudson Bay (Fig. 5a).

Terrestrialization

Our data seem to detect some linkage of terrestrialization rates to climate variation on a millennial scale. As a presupposition terrestrialization frequencies should increase during drier periods (e.g. Nicholson and Vitt, 1994; Ireland et al., 2012; Väliranta et al., 2005). In our data, terrestrialization shows a prominent peak in NE around 10–9 ka (Fig. 6b). This time period coincides with dry conditions and lowered lake levels, especially in Finland and the Baltics (Yu and Harrison, 1995) where terrestrialization was apparently particularly clustered

(Fig. 5b). Terrestrialization frequencies diminish after 9 ka even though warm and dry conditions prevailed widely until 5 ka (Harrison et al., 1996; Wanner et al., 2008; Yu and Harrison, 1995). It must be remembered that the timing and rate of lake level changes as a response to drier climate is strongly affected by local conditions (e.g. Williams et al., 2010). Our data do not suggest that the infilling processes that commenced prior to 9 ka ceased thereafter, but only that *new* sites experiencing peatland initiation through terrestrialization became less common. Therefore, the NE peak of terrestrialization 10–9 ka best indicates the places where local conditions favoured immediate terrestrialization as a consequence of a dry climate.

In NA, terrestrialization seems somewhat consistent between 11 and 3 ka (Fig. 6a). This scatter of terrestrialization frequencies is most likely explained by the slow retreat of the LIS and a regionally variable climate. The Holocene thermal maximum (HTM) -related temperature rise occurred in north-western NA several ka earlier than in the north-eastern part (Kaufman et al., 2004; Renssen et al., 2009). Similarly, the mid-continent experienced time-transgressive early-Holocene droughts moving eastwards between 14–6 ka (Williams et al., 2010). During the early Holocene, terrestrialization seems to have initiated quite quickly in areas where the LIS and Lake Agassiz had retreated (Fig. 5a). The progression of dry climate conditions and subsequent terrestrialization during the early and mid-Holocene is suggested by in our data for the period 11–7 ka (Figs 5a). Interestingly, the strongest NA peak in terrestrialization occurred around 8 ka (Fig. 6a) which coincides with a cluster of rapid responses of various proxies to mid-continental drying as reported by Williams et al. (2010). Terrestrialization that occurred after droughts was mostly an allogenically driven process whereas concurrent terrestrialization caused by slow infilling of, for example, kettle holes left by the retreating ice sheets was autogenic by nature.

Paludification

Peatland initiation via paludification depends on changes in the effective moisture balance (Davis, 1988; Nicholson and Vitt, 1994), and thus paludification frequencies should show a response to millennial-scale Holocene climate variations in our data. However, the climate linkage does not seem straight-forward in NE. Our data show high paludification frequencies during the early Holocene (10–9 ka) especially in the northern parts of Fennoscandia (Figs 5b and 6b) where early-Holocene peatland initiation is well-documented (Juutinen et al. 2013; Mäkilä and Moisanen, 2007; Weckström et al., 2010). Recent studies from Finnish Lapland suggest that during the early Holocene, temperatures were relatively high and that lake levels were not especially high, inferring low relative moisture conditions (Luoto et al. submitted; Siitonen et al., 2011; Väliranta et al., 2005, 2011). Paludification also continued (though decreasingly) through the mid Holocene (8-5 ka) (Fig. 6b) which is generally accepted as a warm and dry climate period in NE (Harrison et al., 1996; Seppä and Hammarlund, 2000; Seppä et al., 2005; Wanner et al., 2008; Yu and Harrison, 1995). Between 6 and 5 ka paludification intensities were at their lowest level (Fig. 6b), which corresponds with the driest mid-Holocene period in NE. Thus, in conclusion, it seems that throughout the early and mid-Holocene the relative moisture conditions remained favourable enough for paludification at least at a regional scale. Alternatively, natural (forest) fire intensity may have increased due to dry a climate (Whitlock and Bartlein, 2003), which may have promoted paludification (Solem, 1989; Tuittila et al., 2007). It has been estimated that in Finland up to 67% of peatlands may actually have formed through paludification initiated after a forest fire (Tolonen, 1983). However, our knowledge of past fire dynamics is still regrettably low (cf. Morris et al., submitted; Sillasoo et al., 2011).

The increase in paludification intensities in conjunction with the Neoglacial cooling and higher effective moisture around NE (e.g., Harrison et al., 1996; Seppä et al., 2005; Siitonen et al., 2011; Snowball et al., 2005; Väliranta et al., 2005; Yu and Harrison, 1995) is evident between 5 and 2.5 ka (Figs 5b and 6b). This intensification of paludification, as a consequence of moister climate conditions and its decrease between 6-5 ka in the driest phase of the Holocene, seem to be the clearest linkages of paludification to climate variation in NE.

In NA the distribution of paludification frequencies is even more diffuse than in NE and no consistent temporal variation exists (Fig. 6a). As with primary mire formation and terrestrialization, the paludification pattern is probably best explained by the vast size of the continent, with paludification frequencies varying over millennia in conjunction with regional climate conditions (e.g. Kaufman et al., 2004; Renssen et al., 2009; Williams et al., 2010). However, a large-scale linkage of paludification to prevailing climate conditions is seen in central NA where early-Holocene drying, driven by a combination of high summer insolation, LIS retreat, Lake Agassiz drainage (Williams et al., 2010) and air circulation patterns (COHMAP, 1988) initially promoted the establishment of forests rather than paludification. Paludification commenced in central NA only with a time-lag of a few thousand years after the ice sheet had retreated (Halsey et al., 1998) (Fig. 5a), possibly promoted by forest fires and/or a moister climate.

Lateral expansion

Lateral expansion can be mainly driven by autogenic processes in relation to the vertical growth and ombrotrophication of peatlands. Such autogenic forcing is not visible in regional age frequency data since peatlands respond to it independently. However, the intensity of lateral expansion can also be linked to allogenic factors, such as climate variation, which should be reflected as a spatially simultaneous increase in basal age frequencies (e.g. Korhola, 1996). On both continents, lateral expansion frequencies increase after 5 ka (Fig. 6). In NE this corresponds with a large-scale climate regime shift towards cooler and moister conditions, i.e. Neoglacial cooling (e.g. Snowball et al., 2005, and references therein). In NA the pattern is not as clear, most probably because of the vast size of the continent and the related spatiotemporal climate variability pattern, but generally the climate became moister after dry early and mid-Holocene phases also in NA (Shuman et al., 2010 and references therein; Wanner et al., 2008). Noteworthy, the lateral spreading was common throughout both continents (Fig. 7), which points to continental scale climate forcing. More specifically, sample grids close to each other in Figure 7 show similar responses, i.e. increasing or decreasing expansion rates, which implies that lateral expansion, on millennial timescales, is mainly driven by sub-continental climate conditions. It seems that only broad-scale climate changes were strong enough to induce continental-wide signals in lateral expansion and to raise the lateral expansion frequencies significantly. At the same time, lateral expansion in NE and NA has also been clearly linked to climate variations on regional scales, with spreading pulses coinciding with cooler and moister climate phases (e.g. Korhola, 1996; Turunen and Turunen, 2003).

Conclusions

We present a data-based synthesis of the proportions, geographical patterns and timing of Holocene peatland initiation processes and lateral expansion. Contrary to previous estimations, all peatland initiation processes seem to have been almost equally common and they largely co-occurred throughout the Holocene. Some geographical patterns are evident, e.g. primary mire formation was mainly restricted to coastal areas.

Our data show that peatland initiation and lateral expansion processes are not necessarily coupled in time or space and are driven by different autogenic and allogenic factors. Primary mire formation seems to be strongly linked to the physical processes of ice sheet retreat and isostatic uplift but positive effective moisture balance has to prevail at the site. Terrestrialization seems to be autogenically (infilling) driven on millennial timescales and at the same time climate-driven (dry periods) on shorter timescales. Paludification slowed down in NE during the driest Holocene phase between 6–5 ka but otherwise it has been a continuous process over all northern latitudes throughout the Holocene. The data suggest that lateral expansion is also linked to climatic conditions as it accelerated during the generally cooler and moister late Holocene. It should be noted that the formation of new peatland areas does not necessarily decrease when the initiation rates decrease but that new peatland areas are continuously formed via lateral expansion.

Our data indicate a connection between peatland development on continental scales to millennial-scale climatic variations. However, it seems that detailed linkages are better observed and validated on regional scales because climatic variations are rarely uniform over wide areas and local conditions determine how they affect peatland formation.

There has been much debate on the future fate of peatlands and their carbon dynamics in relation to climate change. It is difficult to estimate the effects of climate change on the northern peatland complex as a whole since the estimated changes in temperature and precipitation vary significantly over the northern hemisphere. Modern experimental peatland studies, combined with palaeoecological information of past spatiotemporal changes in peatland environments, may elucidate possible functional responses of peatlands to predicted changes in climate. In order to assess the future carbon dynamics of peatlands it is crucial to understand the controlling factors behind spatiotemporal changes in initiation, lateral expansion and variations in the areal extent of peatlands. These factors must be considered in the discussion of future peatland dynamics and in the linking of northern peatlands to global climate–carbon cycle models.

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Figures

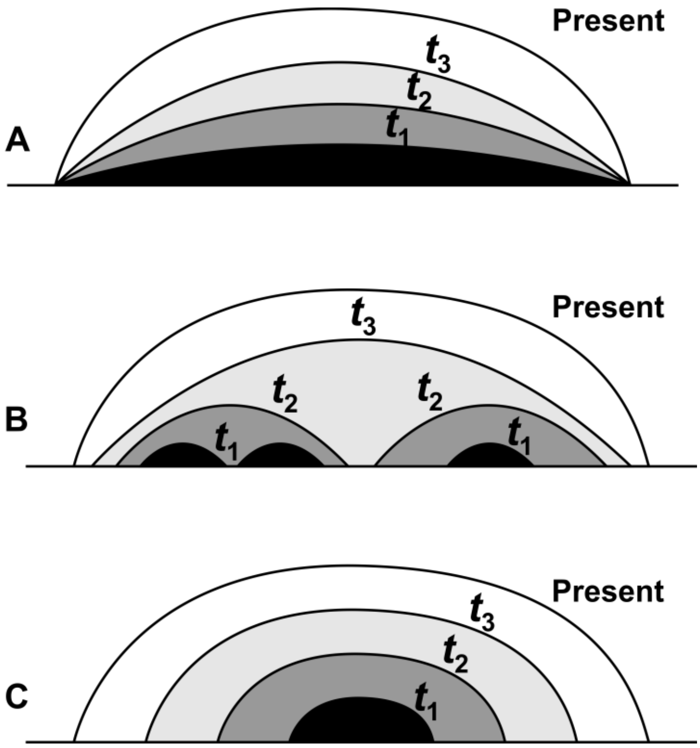

Figure 1. Three conceptual models of raised bog development at different times (t) leading to the present state (from Foster and Wright, 1990). In A, the peatland has initiated over a wide area almost simultaneously and has not subsequently spread laterally but has accumulated peat vertically. In B, the peatland extant at present has initiated from multiple loci, possibly at different times and through different initiation processes, that have later fused together through lateral expansion. In C, the peatland has initiated from one locus and has spread laterally uniformly through time while also growing vertically.

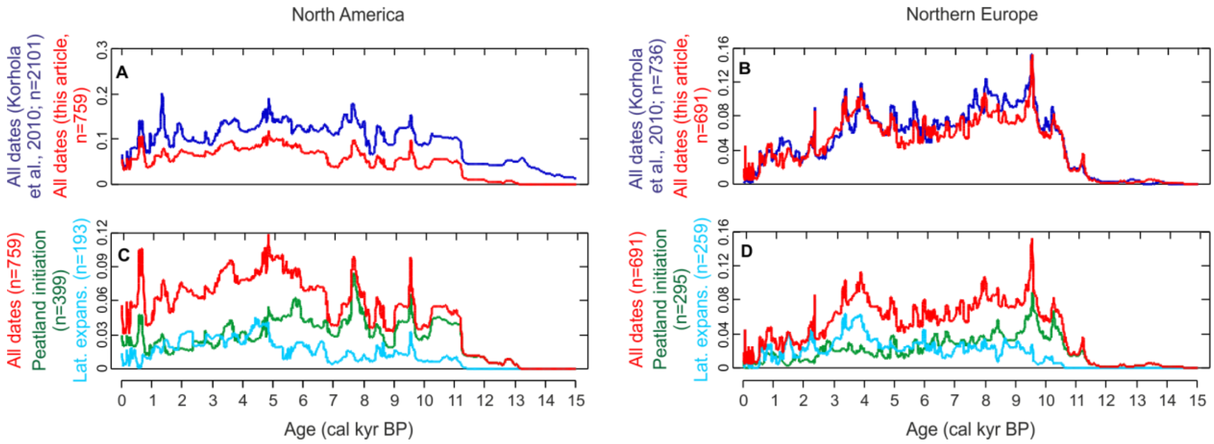

Figure 2. Comparison of the present data-set to all available basal peat ages in North America and northern Europe and the composition of the data-set as summed probability curves. A) and B) the frequencies of basal peat dates in the present data-set (red) compared to all available basal peat dates (blue) (data from Korhola et al., 2010) in North America and Europe, respectively. C) and D) the composition of the present basal peat data-set, i.e. all basal peat dates (red) vs. peatland initiation dates (green) and lateral expansion dates (light blue) in North America and northern Europe, respectively.

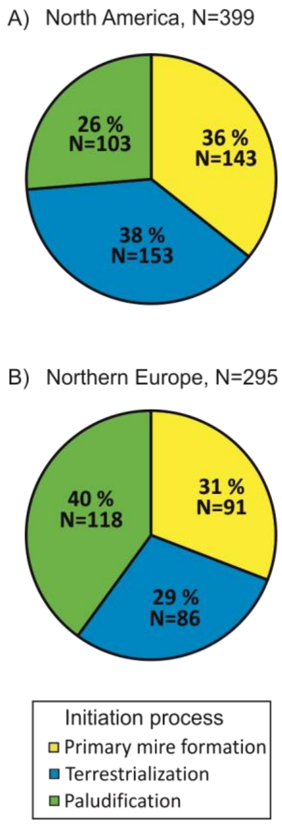

Figure 3. Relative proportion of peatland initiation processes in North America and northern Europe. A) North America (N= 399) and B) northern Europe (N= 295).

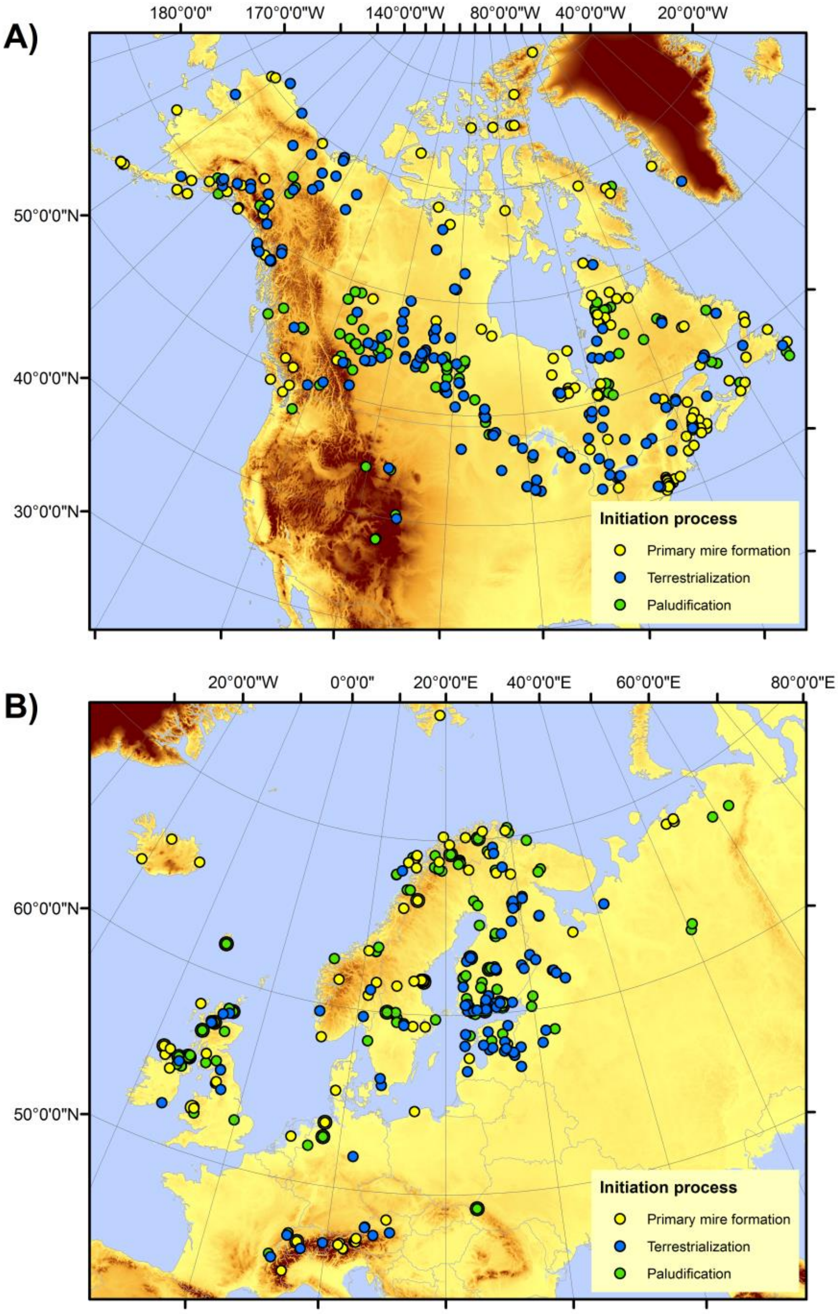

Figure 4. Spatial distribution of peatland initiation processes in North America and northern Europe. A) North America (N=399) and B) northern Europe (N=295). Elevation data is from ETOPO1 (Amante and Eakins, 2009).

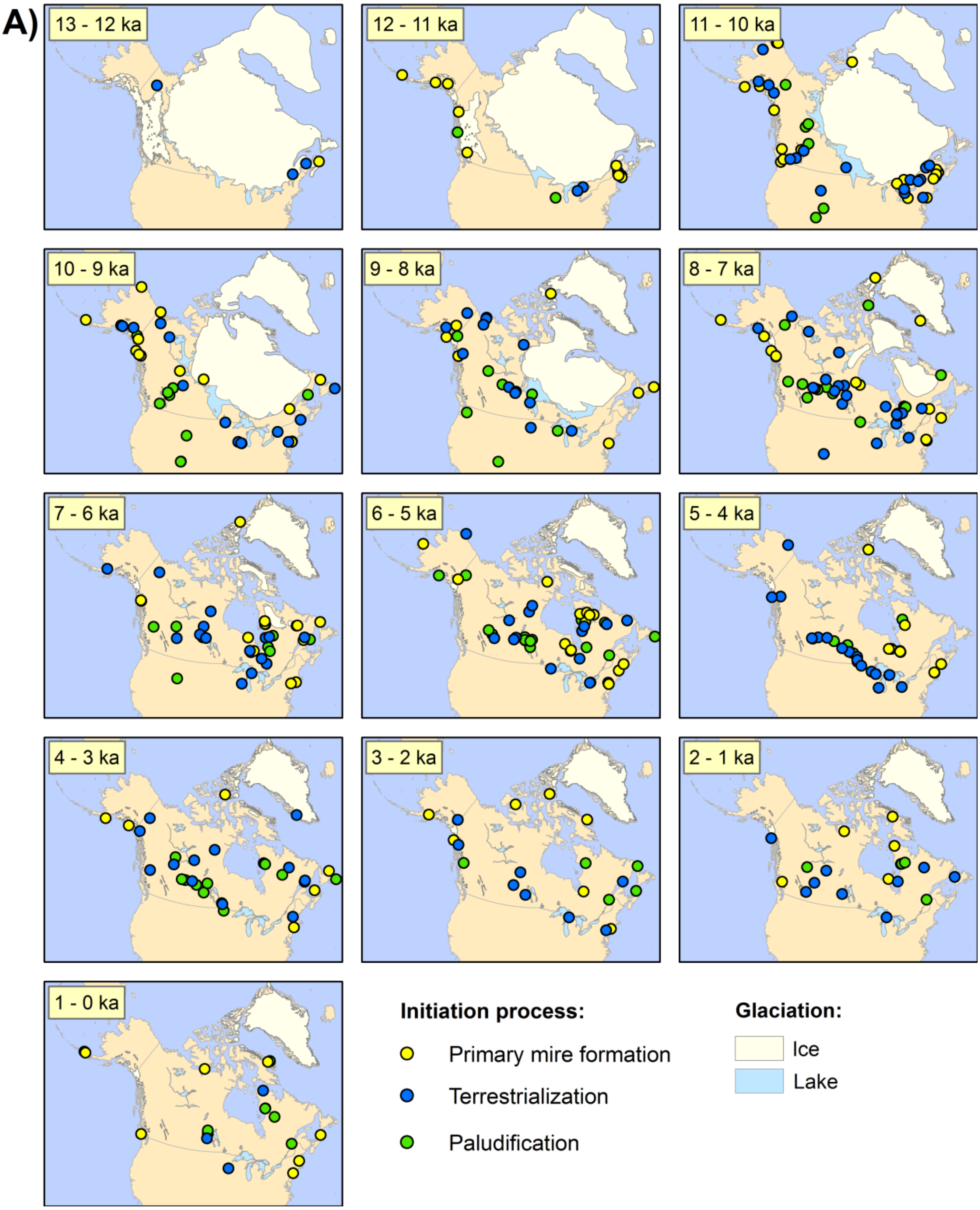

Figure 5 continues on next page.

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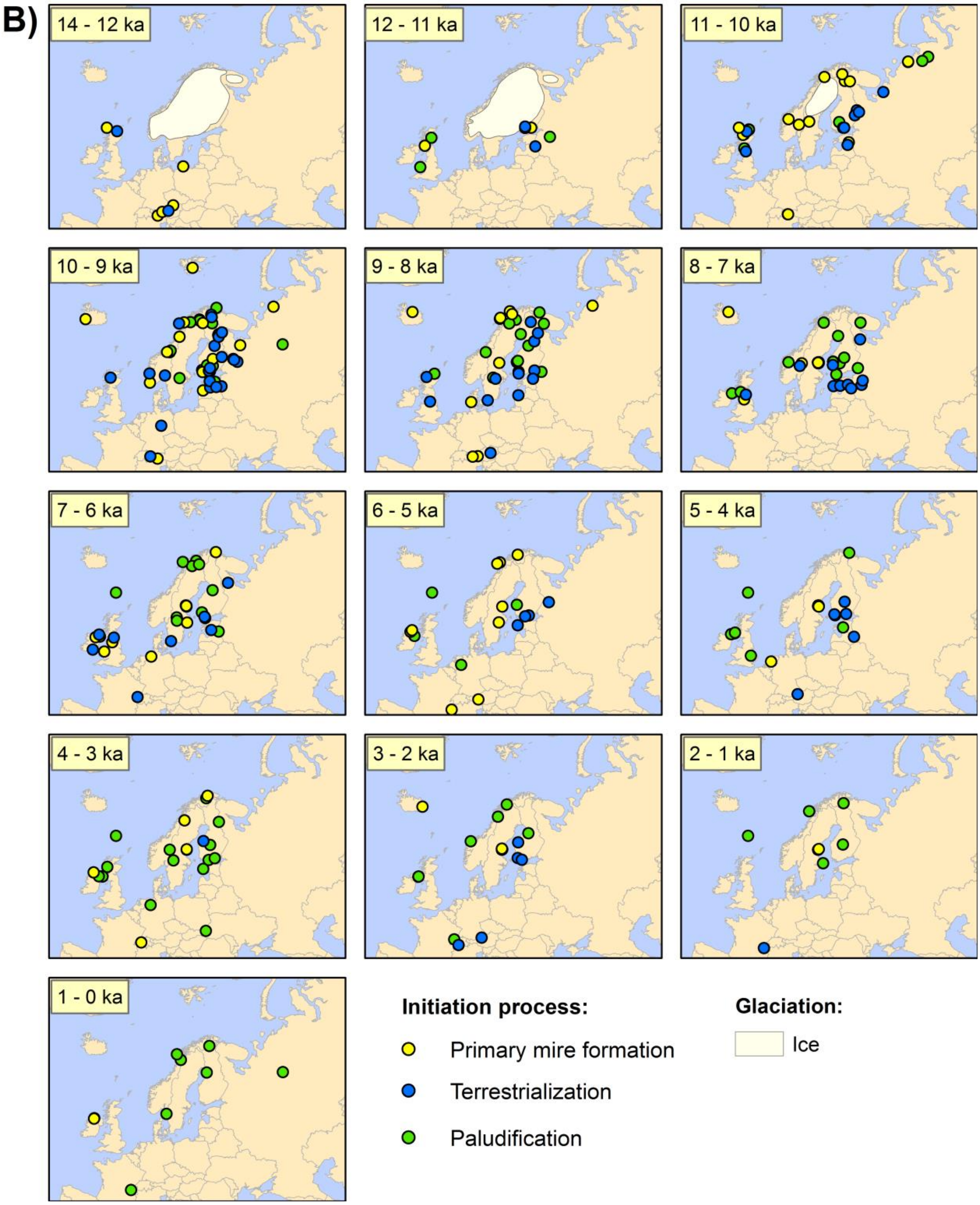

607 Figure 5. Time and location of the peatland initiation processes in North America and
608 northern Europe during the Holocene in 1000 year time slices. A) North America (N=399)
609 and B) northern Europe (N=295). The glaciation data for North America is from Dyke et al.,
610 2003 (GIS data source: http://www.mcgill.ca/library/library-findinfo/maps/deglaciation/)
611 while northern Europe data was digitized from Eronen et al. (2001).

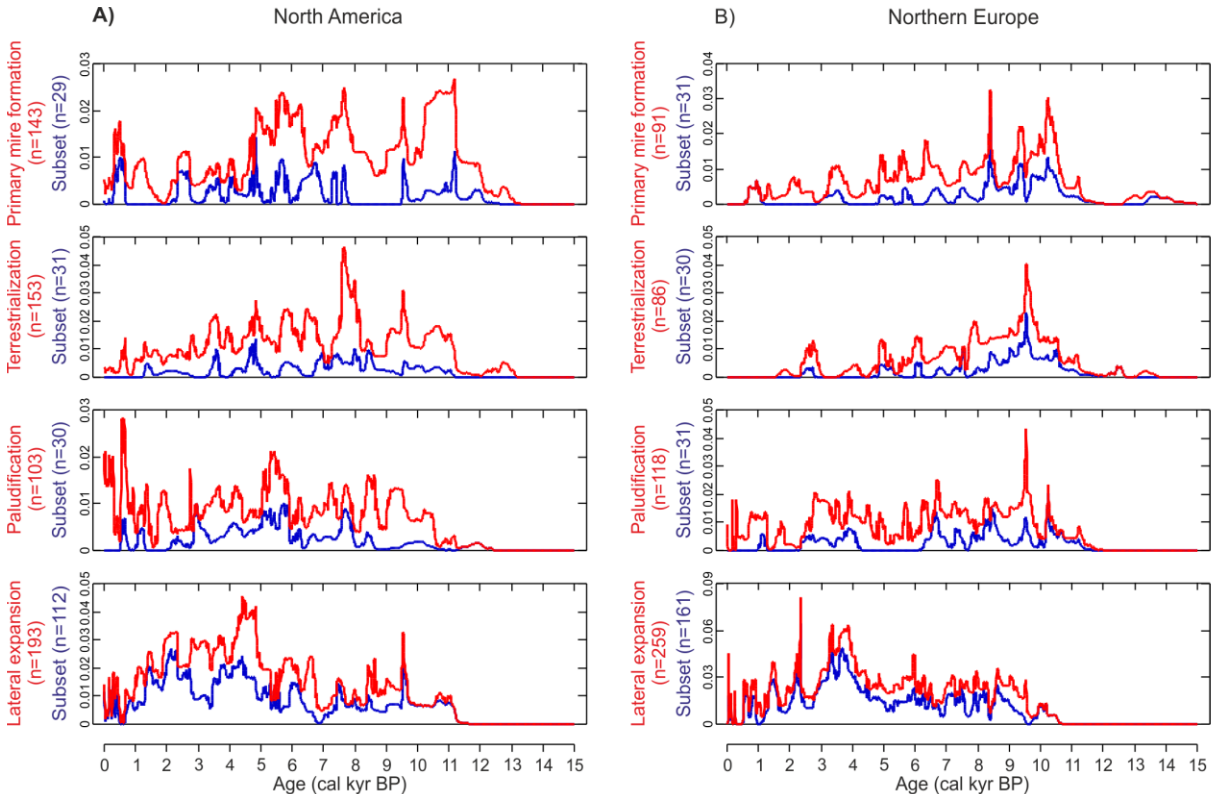

Figure 6. Occurrence frequencies of the peatland initiation processes and lateral expansion during the Holocene as summed probability curves in A) North America and B) northern Europe. In the case of the initiation processes, N depicts the number of observations/peatlands for each process. The red curve shows the trends of all dates per initiation process whereas the blue curve represents a subset of the most reliable interpretations of the respective initiation process. In the case of lateral expansion, N depicts the number of horizontal spread observations from multiple-dated peatlands. The red curve shows trends from peatlands with ≥ 3 lateral expansion dates per peatland whereas the blue curve represents expansion dates from peatlands with ≥ 7 lateral expansion dates.

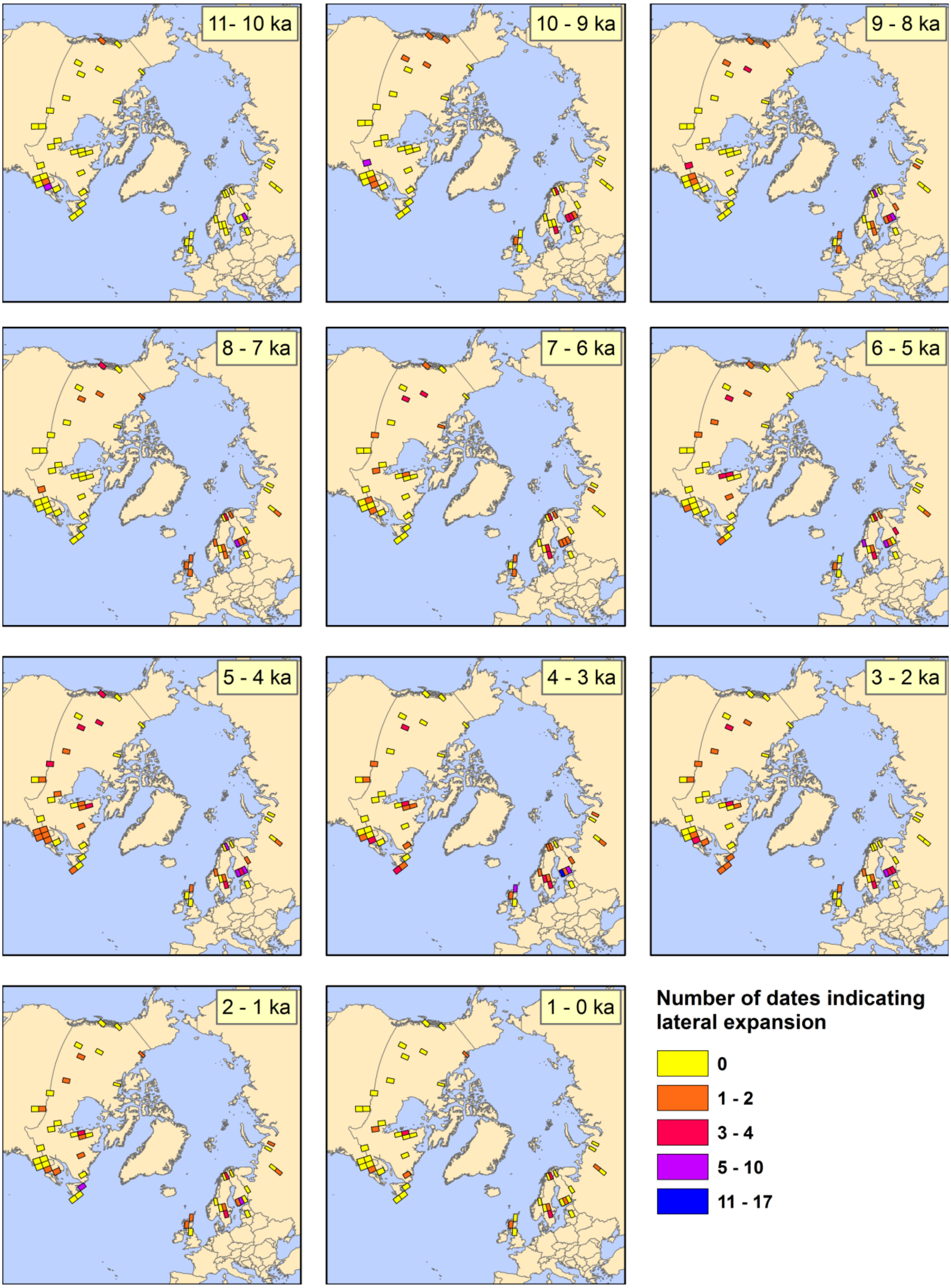

Figure 7. Lateral expansion dynamics of existing peatlands in North America and northern Europe. The study area has been divided into 2×2° cells. The grid colour indicates the number of lateral expansion dates inside the cell during a certain time interval, irrespective of

the number of individual peatland sites inside the cell. Light yellow cells indicate cells that generally contain observations from laterally spreading peatlands, but do not contain any expansion dates in the time frame in question. N = 452 from 116 peatlands.

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